A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 96: 89–104 (2024)
DOI: 10.3897/neobiota.96.122752

Research Article

Evaluation of climate conditions and ecological traits that limit the distribution expansion of alien *Lolium rigidum* in Japan

Kentaro Uehira[1], Yoshiko Shimono[1]

1 *Graduate School of Agriculture, Kyoto University, Kitashirakawaoiwake-cho, Sakyo-ku, Kyoto, 606-8502 Japan*
Corresponding author: Kentaro Uehira (uehirak789@yahoo.co.jp)

Abstract

Invasive alien plants cause severe global problems; therefore, determining the factors that lead to the success or failure of invasion is a critical question in the field of invasion ecology. In this study, we aimed to determine the factors underlying differences in the distribution range of alien plants in Japan by investigating why *Lolium multiflorum* thrives in a wide range of habitats while *L. rigidum* is mainly distributed on sandy beaches. We initially evaluated environmental niche suitability through species distribution modelling and subsequently examined whether species traits influence the differences in range expansion between the two species. We used MaxEnt modelling to identify potential environmental niches for both species. The analysis revealed that *L. rigidum* was considerably less suited to the Japanese climate compared to *L. multiflorum*, with high summer precipitation in Japan identified as one of the climatic factors limiting the distribution of *L. rigidum*. Given that these winter annual plants remain dormant as seeds during summer, in subsequent experiments, we buried seeds in paddy field soil and sandy beach sand during summer and evaluated their survival rate in autumn. The survival rate of *L. rigidum* seeds was significantly lower than that of *L. multiflorum*, particularly in paddy soil. Factors contributing to seed mortality may include the decay or early germination of *L. rigidum* seeds under Japan's high rainfall conditions. This study emphasises the importance of considering local environmental factors alongside climate niche modelling in the risk assessment of invasive species. Moreover, the integration of species distribution modelling for large-scale evaluations and manipulation experiments for fine-scale assessments proved effective in identifying climatic conditions and species traits influencing the success or failure of alien species invasion.

Key words: Coastal environment, invasion success, local environmental condition, MaxEnt, seed burial experiment, seed decay, species distribution modelling, summer rainfall

OPEN ACCESS

Academic editor: Elizabeth Wandrag
Received: 11 March 2024
Accepted: 2 September 2024
Published: 31 October 2024

Citation: Uehira K, Shimono Y (2024) Evaluation of climate conditions and ecological traits that limit the distribution expansion of alien *Lolium rigidum* in Japan. NeoBiota 96: 89–104. https://doi.org/10.3897/neobiota.96.122752

Introduction

Invasive alien plants cause issues such as loss of biodiversity, reduced crop yield, and health risks (Vitousek 1990; Pyšek and Richardson 2010; Vilà et al. 2010). However, not all introduced species become invasive in a new habitat. It has been hypothesised that only about 10% of species successfully progress through the consecutive steps of the invasion process. Specifically, approximately 10% of species transported beyond their native range will be released or escape in the new regions, about 10% of these introduced species will successfully establish themselves, and about 10% of established species will become invasive (tens rule; Williamson and Fitter 1996). Therefore, extensive long-term research has been conducted to

identify which environments facilitate the establishment of invasive species and which species' characteristics contribute to the successful establishment (Richardson and Pyšek 2006; Hayes and Barry 2008; Hui et al. 2016).

The impact of climate on determining invasion success or failure has been extensively investigated using the species distribution modelling (SDM) approach. This approach can estimate suitable climate conditions for a target species based on historical climate and species occurrence data and predict the distribution suitability of the species across geographic and temporal scales. This approach has revealed that specific climate factors can influence the potential geographic distribution of a species (Phillips et al. 2006; Phillips and Dudík 2008; Wiens et al. 2009). SDM is widely used in the risk assessment of invasive species, largely because the climatic niche of invasive species in their new destination areas often resembles that in their source areas (Liu et al. 2020). Although SDM is a robust tool that combines statistical modelling and geographic information systems to gain insights into the potential environmental factors influencing species distributions (Phillips et al. 2004), it cannot definitively establish causal relationships between environmental factors and species distribution (Merow et al. 2013). To identify the drivers of invasion processes in destination areas, experiments manipulating environmental factors are necessary; however, few studies have combined both SDM and experimental manipulation approaches.

The genus *Lolium* includes two outcrossing annual species: *L. multiflorum* Lam. and *L. rigidum* Gaudin, which are native to the Mediterranean region (Terrell 1968). They have been introduced as a forage crop and turfgrass in numerous countries across the globe (Humphreys et al. 2010), resulting in their escape from controlled areas and becoming problematic weeds. *L. multiflorum* is widely distributed throughout Europe, North America, South America, northern and eastern Africa, Australia, Central Asia, and eastern Asia (GBIF 2022a) (Fig. 1a). It directly reduces crop yield by spreading as a weed in agricultural fields (Liebl and Worsham 1987; Sønderskov et al. 2020) and serving as a habitat for rice-ear bugs, which are important pests of rice (Yoshioka et al. 2011). *L. rigidum* is distributed throughout Europe, Australia, North America, South America, South Africa, East Asia, and West Asia (GBIF 2022b) (Fig. 1b). This species has developed tolerance to multi-

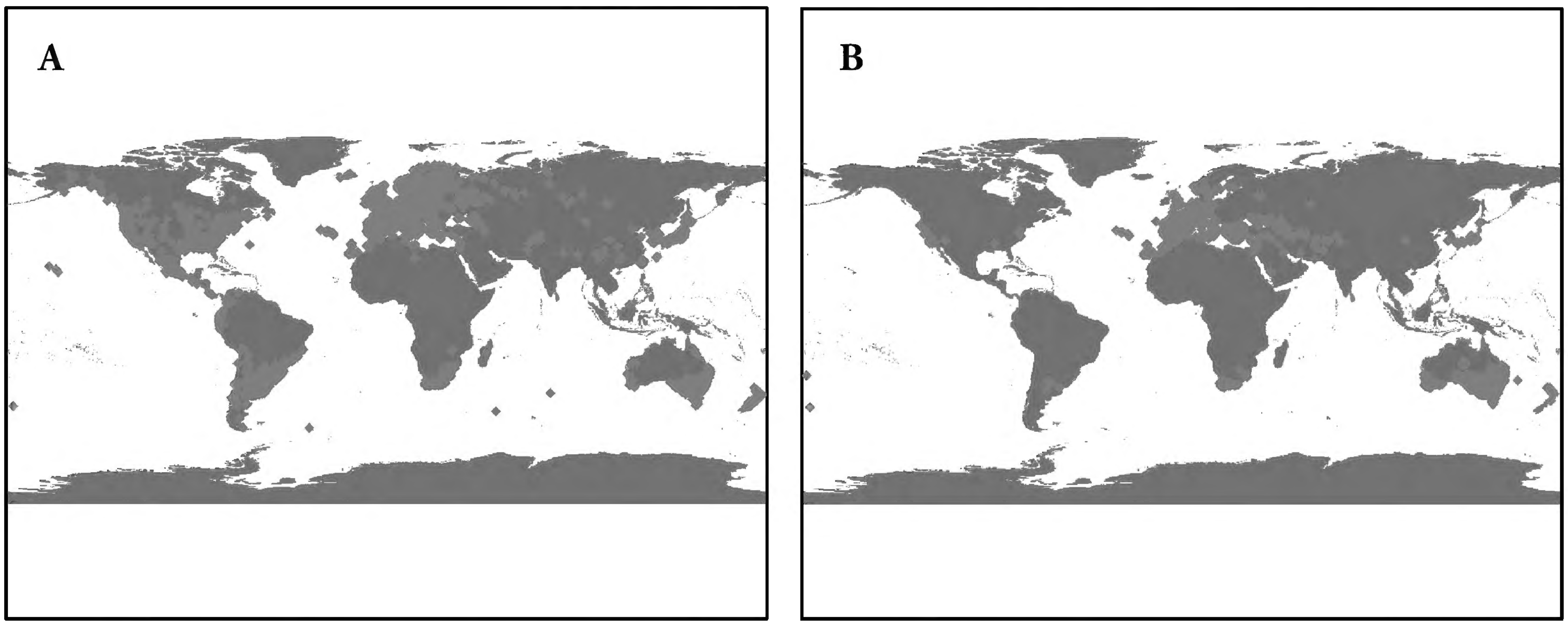

Figure 1. The distribution of **A** *L. multiflorum* and **B** *L. rigidum*. This distribution map was made using the occurrence data from GBIF (GBIF 2022a, 2022b).

ple herbicides, posing a serious challenge (Heap 2023), particularly in wheat cultivation in Australia (Owen et al. 2014). In Japan, *L. multiflorum* has predominantly been introduced as forage and revegetation materials but has spread as weeds in universal environments such as farmland and riverbanks. Conversely, *L. rigidum* has mainly been introduced to Japan through imported grains contaminated with *L. rigidum* seeds and subsequently became established (Shimono et al. 2015; Higuchi et al. 2017; Hirata et al. 2023). Originally a weed in agricultural fields, it has only been specifically established in local environments, such as sandy beaches, in Japan (Hirata et al. 2023).

In this study, we aimed to investigate environmental factors and species traits that contribute to the distribution expansion of alien plants in Japan using both SDM and manipulation experiments, focusing on congeneric species of the genus *Lolium* with different distribution ranges in Japan. Specifically, we investigated why *L. multiflorum* thrives in a wide range of habitats whereas *L. rigidum* has not been able to spread to agricultural fields. We initially examined the suitability of the climate in Japan for the spread of these *Lolium* species using the MaxEnt model (Phillips et al. 2006), which is the most common SDM approach. MaxEnt analysis revealed summer precipitation as a key climatic factor limiting the distribution of *L. rigidum* in Japan. In addition, as *L. rigidum* and *L. multiflorum* are winter annuals that exist as seeds during the summer, we evaluated the seed survival rates of both *Lolium* species in the soil from summer to autumn.

Methods

Species distribution modelling

Global distribution data for *L. multiflorum* and *L. rigidum* were acquired from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) in July 2022 (GBIF 2022a, 2022b). Although the GBIF data contained accurate information on the coordinates, we used all the data without specifying it. This approach helps us avoid the risk of simultaneously losing data from specific regions that would have been lost had we specified the accuracy of the coordinates. As environmental data, we used 19 bioclimatic variables worldwide derived from temperature and precipitation records from 1970 to 2000 (See Suppl. material 1: table S1), sourced from the WorldClim database (https://www.worldclim.org/) (Fick and Hijmans 2017). This dataset is frequently used for ecological studies focusing on SDM (Booth et al. 2014). The raster data resolution was set to 10 min. Duplicated occurrence points were eliminated in the modelling process, resulting in one occurrence point per cell. As a result, 4,099 and 9,040 points were retained for *L. rigidum* and *L. multiflorum*, respectively.

According to Phillips (2008), 10,000 'background' (or 'pseudo-absence') points are typically sufficient for MaxEnt modelling. However, the number should be sufficient to adequately account for the range of climate variability in the study area, and > 10,000 points may be needed for a large number of occurrence records. In accordance with this recommendation, the background for this study, involving an expansive area and a large number of occurrence records, was set at 30,000 for *L. rigidum* and 50,000 for *L. multiflorum.* Model performance can be further improved by restricting the occurrence of background points to fractions containing occurrence points (Phillips 2008; Anderson and Raza 2010). Therefore, we limited

the occurrence of background points to locations within a radius of 500 km from the occurrence points of *Lolium* species.

We implemented variable selection in the subsequent steps because of multicollinearity among environmental variables potentially decreasing prediction accuracy (Heikkinen et al. 2006; Dormann et al. 2013). Firstly, we calculated the Pearson correlation matrix for all combinations of variables. Secondly, we utilised the MaxEnt v.3.4.3 software to run a MaxEnt model with all 19 variables. Then, we extracted variable pairs with a correlation coefficient > 0.7, as per the criteria set by Green (1979). The variable with a smaller contribution to the MaxEnt model was then removed based on the variable importance of MaxEnt output. Finally, the MaxEnt model was reconstructed using only the remaining variables. We conducted five-fold cross-validation and assessed goodness of fit using the area under the receiver operating characteristic (ROC) curve (AUC) value, which ranges from 0 to 1; a value of 0.5 indicates random guessing, whereas a value of 1 signifies perfect classification (Fielding and Bell 1997). A response curve was created for each variable (meaning that a predictive model was created for each variable), and the contribution of each variable to the model was evaluated using a jackknife test (both are built-in functions of the MaxEnt software). The response curve was overlaid with the density distribution of the corresponding climate variable in Japan. Other MaxEnt settings were set as default.

To identify the environmental variables impacting the suitability of *Lolium* species in Japan, we set one Japanese climate variable to the optimal value determined from MaxEnt output response curves while keeping the remaining variables at their original values to simulate changes in distribution suitability. MaxEnt was performed for each value-adjusted variable using the same parameter settings as mentioned above.

Seed burial experiment

L. rigidum and *L. multiflorum* are both winter annuals, germinating in autumn, flowering in spring, and dispersing seeds in early summer. Therefore, seed burial experiments were performed to assess their survival rates from summer to autumn. In June 2021, mature seeds of *L. rigidum* and *L. multiflorum* were collected from naturalised populations along a sandy beach (34.7923°N, 136.558°E) and the levee of a paddy field (34.7991°N, 136.5342°E) in Mie Prefecture. Paddy soil consisting mainly of clay was collected from the experimental field at Kyoto University (35.0321°N, 135.7835°E) and beach soil was collected at 5-cm depths on seven sandy beaches in central Japan (Suppl. material 1: table S2), where *L. rigidum* growth was confirmed. We used sandy beach soils collected from multiple locations because the sand grain size varies depending on the location.

Fifty seeds of each species were packed into non-woven fabric bags (length: 9 cm; width: 7 cm) that also contained 5.0 g of autoclaved paddy soil or beach sand to prevent the seeds from adhering to each other. One bag containing each species was buried at depths of 7 cm and 15 cm in plastic pots (diameter: 16.8 cm; height: 19.8 cm) filled with paddy soil and beach soil in July 2021, respectively. There were three and seven replications per species for beach soil and paddy soil, respectively. Intense sand movement by strong wind in sandy beaches and tillage in paddy fields results in seeds being buried at varying depths. Therefore, to investigate whether differences in burial depth affect survival rates, two burial depths

were set in this study. The plastic pots were placed on the experimental field at Kyoto University, remained exposed to rainfall, and then retrieved in October of the same year, coinciding with the germination period under natural conditions. The precipitation from July to October 2021 was 390 mm (July), 468 mm (August), 180 mm (September), and 41 mm (October) (Japan Meteorological Agency 2024).

Additionally, in 2024, similar experimental setups were conducted using paddy soil from Kyoto University and sandy beach soil collected in Mie Prefecture (34.7923°N, 136.558°E), measuring soil moisture contents (%) from June to July using digital handheld moisture meter (PMS-714, Omega Engineering inc.).

Seeds were collected from the soil, and those without hard embryos were discarded. Traces of rooting were checked. The remaining seeds were placed on 9.0-cm Petri dishes and germinated in an incubator (LH-30-8CT, Nippon Medical & Chemical Instruments) at 30/20 °C with alternating 12/12 h cycles (i.e., 12 h light and 12 h dark) for a week. These conditions were based on Rodriguez et al. (1998). Finally, we used the 2,3,5-triphenyltetrazolium chloride (TTC) method to differentiate between dormant and dead seeds with ungerminated, hard embryos. The seeds were bisected to expose the embryo, then immersed in a 1% TTC solution, and incubated overnight at 25 °C in the dark. The following morning, we examined the seeds to determine whether the embryos had been stained. The total number of viable seeds during the burial period was calculated by summing the number of individuals that had already germinated in the soil (but were alive at the time of retrieval), those that germinated in the incubator, and those that were stained by the TTC method. The total number of dead seeds was calculated by summing the number of individuals that lacked hard embryos (including those that showed traces of germination and had already died) and those that were not stained by the TTC method.

A hierarchical linear model with binomial errors was employed to evaluate the survival rate of *Lolium* spp. seeds. The primary effects examined in this study were *Lolium* spp., soil type (paddy or beach soil), and burial depth, whereas the random effects were plastic containers and beach soil collection sites. Statistical analysis was performed using the rstan package (Stan Development Team 2024) in R ver. 4.2.3 (R Core Team 2023).

Results

Species distribution modelling

After variable selection, eight variables remained for *L. rigidum*: mean diurnal range (bio2), temperature seasonality (bio4), mean temperature of the wettest quarter (bio8), mean temperature of the warmest quarter (bio10), precipitation seasonality (bio15), precipitation of the driest quarter (bio17), precipitation of the warmest quarter (bio18), and precipitation of the coldest quarter (bio19). Similarly, seven variables remained for *L. multiflorum*: annual mean temperature (bio1), mean diurnal range (bio2), temperature annual range (bio7), mean temperature of the wettest quarter (bio8), precipitation of the wettest month (bio13), precipitation seasonality (bio15), precipitation of the coldest quarter (bio19) (See Suppl. material 1: table S3 for correlation coefficients and Suppl. material 1: table S4 for variable contributions).

The average AUC values were 0.77 and 0.82 for *L. rigidum* and *L. multiflorum*, respectively. These values are considered moderately predictive according to the AUC criteria described by Vanagas (2004). The jackknife test showed that the most useful and unique information for predicting the global distribution was temperature seasonality (bio4) for *L. rigidum* and annual mean temperature (bio1) and temperature annual range (bio7) for *L. multiflorum* (Fig. 2).

Based on the MaxEnt model of *Lolium* species projected for Japan, the mean probability of *L. rigidum* presence was 0.055 (SD: 0.035), whereas that for *L. multiflorum* was 0.31 (SD: 0.076) (Fig. 3).

Fig. 4 displays the response curves and density distributions of both *Lolium* species in Japan for each bioclimatic variable. Japanese climate varies considerably from the optimum ranges for *L. rigidum* in terms of temperature seasonality (bio4) and precipitation of the warmest quarter (bio18) and for *L. multiflorum* in the mean temperature of the wettest quarter (bio8).

When Japanese bioclimatic variables were fixed to the values that maximise suitability for *L. rigidum*, which had a particularly low probability of presence in Japan, in the response curves, changes in mean diurnal range (bio2), mean temperature of the wettest quarter (bio8), mean temperature of the warmest quarter (bio10),

A

B

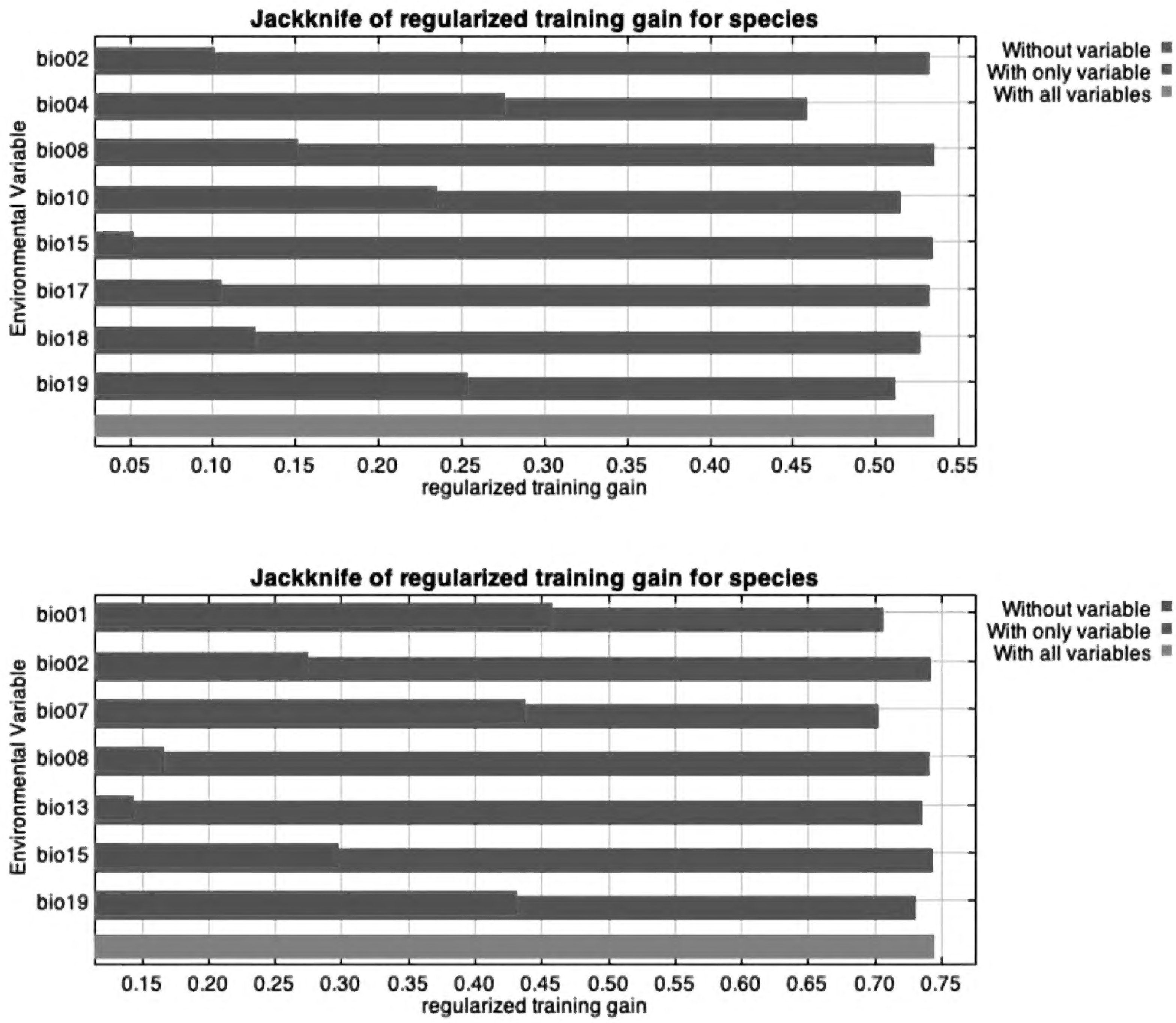

Figure 2. Relative predictive power of each bioclimatic variable based on the regularised training gain in MaxEnt models, as estimated using the jackknife test, for **A** *L. rigidum* and **B** *L. multiflorum*.

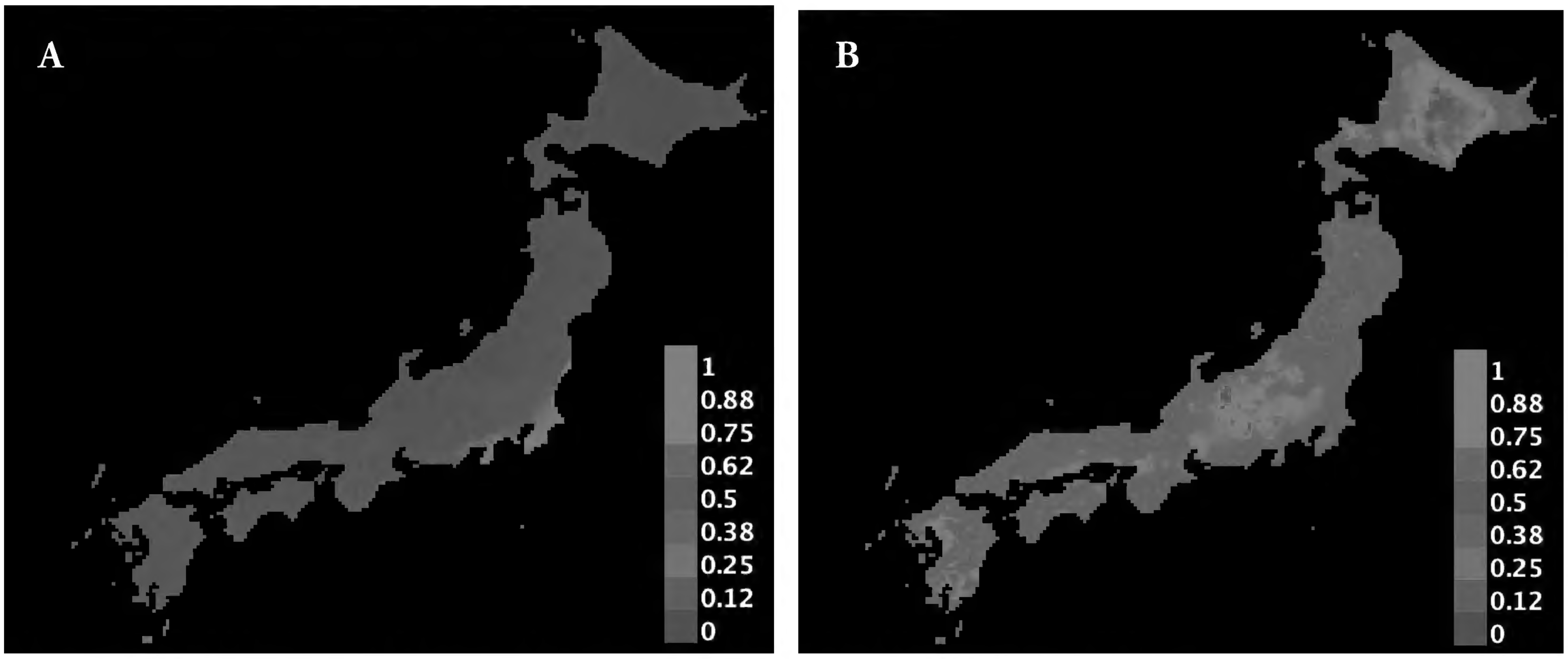

Figure 3. Probability of presence in Japan estimated by MaxEnt for **A** *L. rigidum* and **B** *L. multiflorum.*

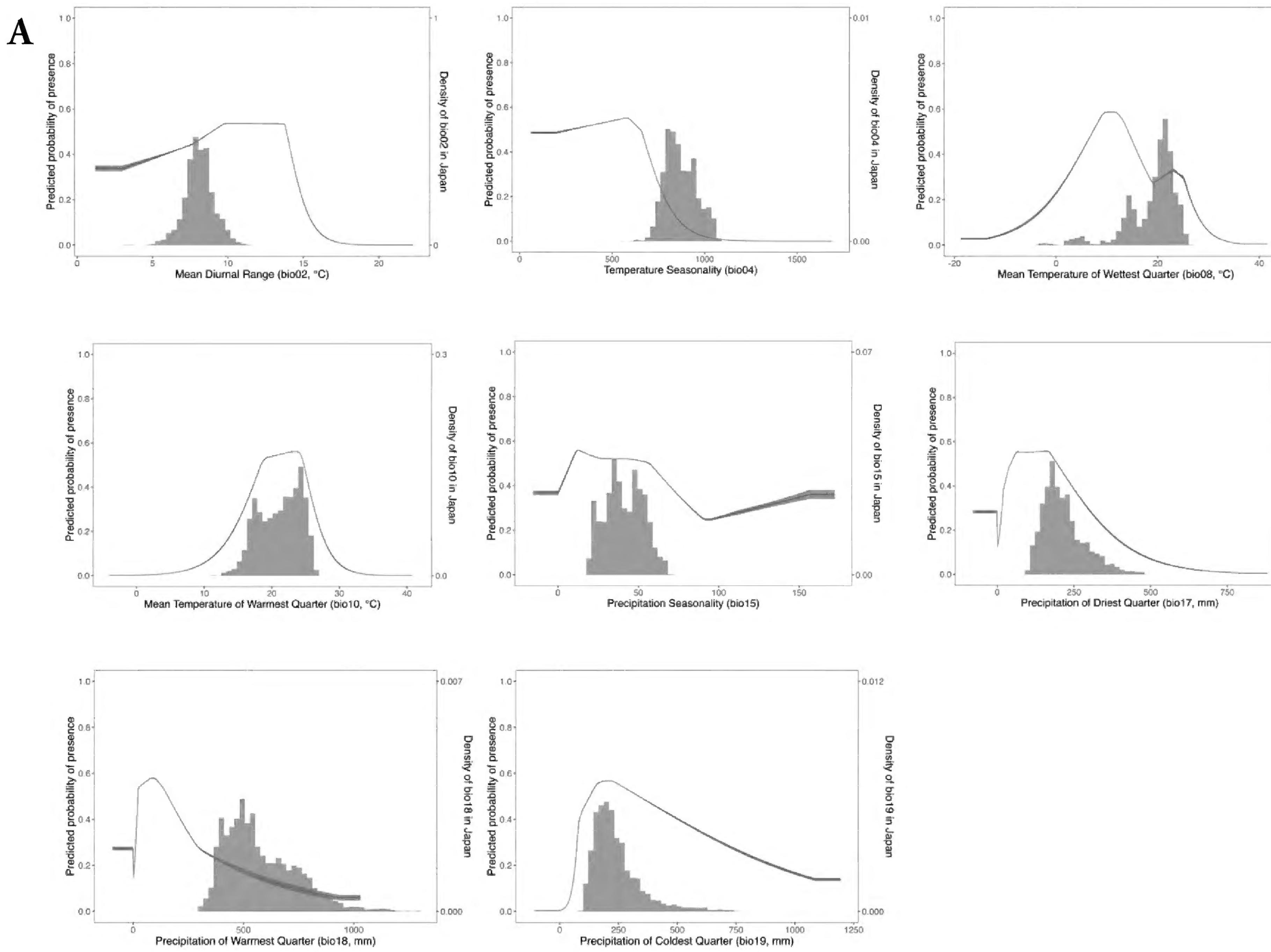

Figure 4. **A** response curves for *L. rigidum* (red lines and blue shades) and density distributions of Japanese bioclimatic variables (green histograms) **B** response curves for *L. multiflorum* (red lines and blue shades) and density distributions of Japanese bioclimatic variables (green histograms). The horizontal axis displays the variation range of the bioclimatic variables. The first vertical axis shows the predicted suitability of the target species, while the second vertical axis shows the density distribution of Japanese bioclimatic variables. The red line represents the mean of the five iterations of the estimation, while the blue shade indicates its standard deviation.

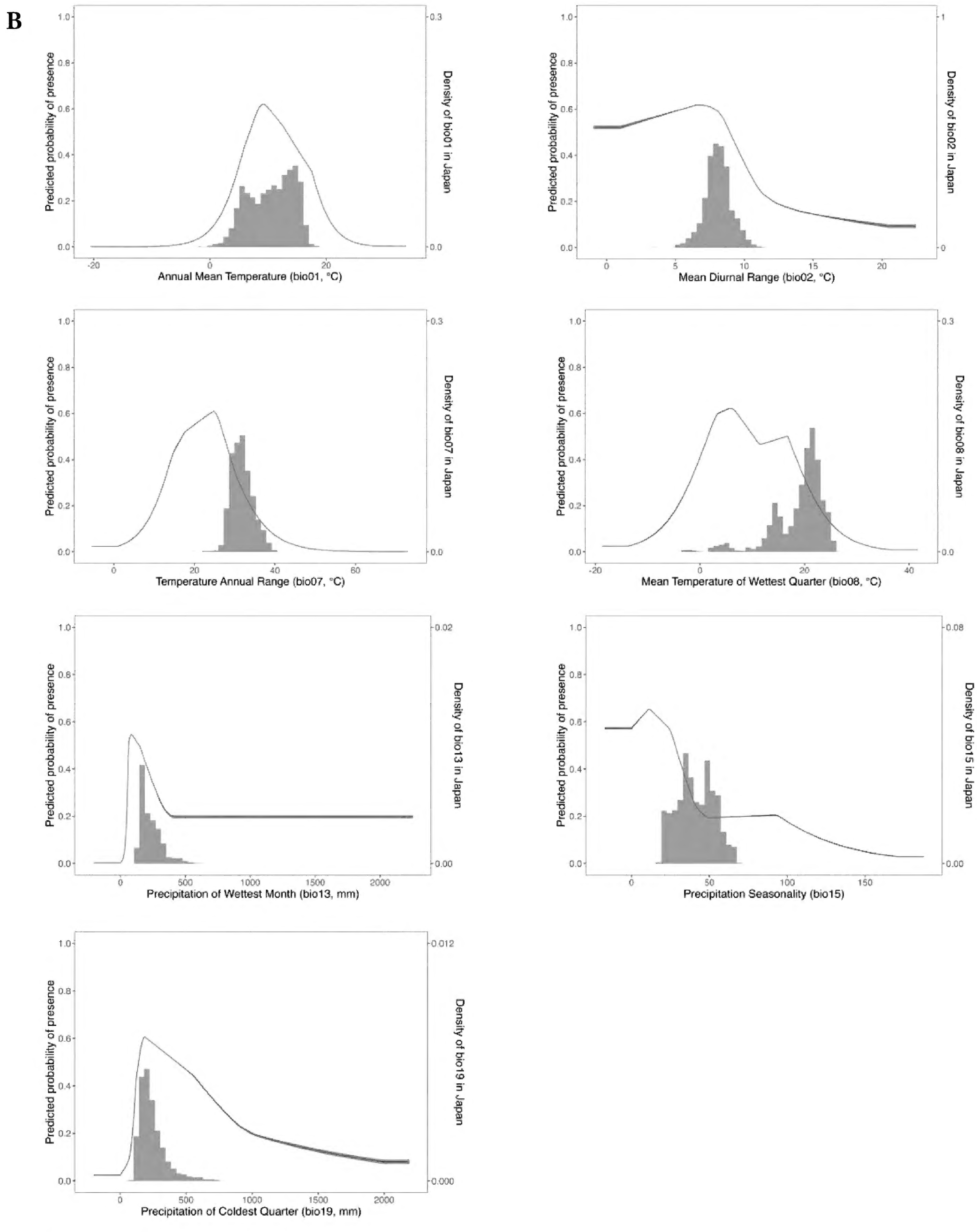

Figure 4. Continued.

seasonality of precipitation (bio15), precipitation in the driest month (bio17), and precipitation in the coldest month (bio19) had minimal impact on the probability of the presence in Japan, with mean values of 0.055, 0.058, 0.055, 0.051, 0.046, 0.058, respectively (Suppl. material 1: fig. S1). Conversely, temperature seasonality (bio4) and precipitation of the warmest quarter (bio18) increased the probability of presence to mean values of 0.28 (SD: 0.038) and 0.26 (SD: 0.14), respectively (Fig. 5).

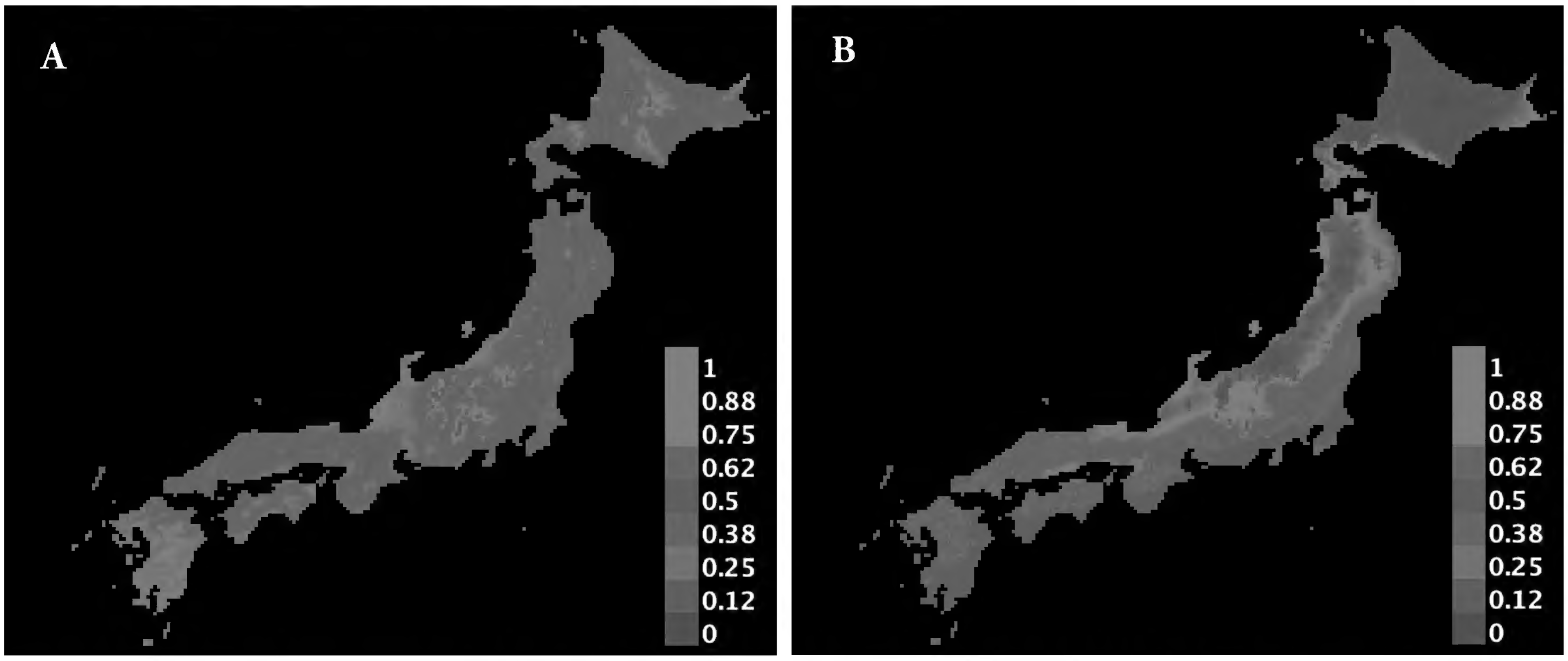

Figure 5. Probability of presence estimated by Maxent for *L. rigidum* when the bioclimatic variables fixed at their optimum values **a** shows bio04 and **b** shows bio18.

Seed burial experiment

The diurnal variation of soil moisture contents for 1 month (from June 22nd to July 20th, 2024) revealed that the soil moisture of beach soil decreased rapidly in the absence of rain, and, on all days, the soil moisture was higher in paddy soil than in beach soil (Fig. 6). An average of 94% (SD: 4.1%) of seeds were retrieved from soil-filled bags. The average seed survival rates of *L. rigidum* and *L. multiflorum* were 63% and 79%, respectively (Fig. 7). Hierarchical linear model results showed that *L. rigidum* had a significantly lower seed survival rate than that of *L. multiflorum* and that the seed survival rate was significantly higher in sandy beach soils than that in paddy soils, with a minor impact of burial depth (Fig. 8a). The model-estimated survival rates of both *Lolium* spp. at different depths in paddy and beach soils indicated that the seed survival rate of *L. rigidum* in paddy soil was the lowest among all combinations, dropping below 50% (Fig. 8b).

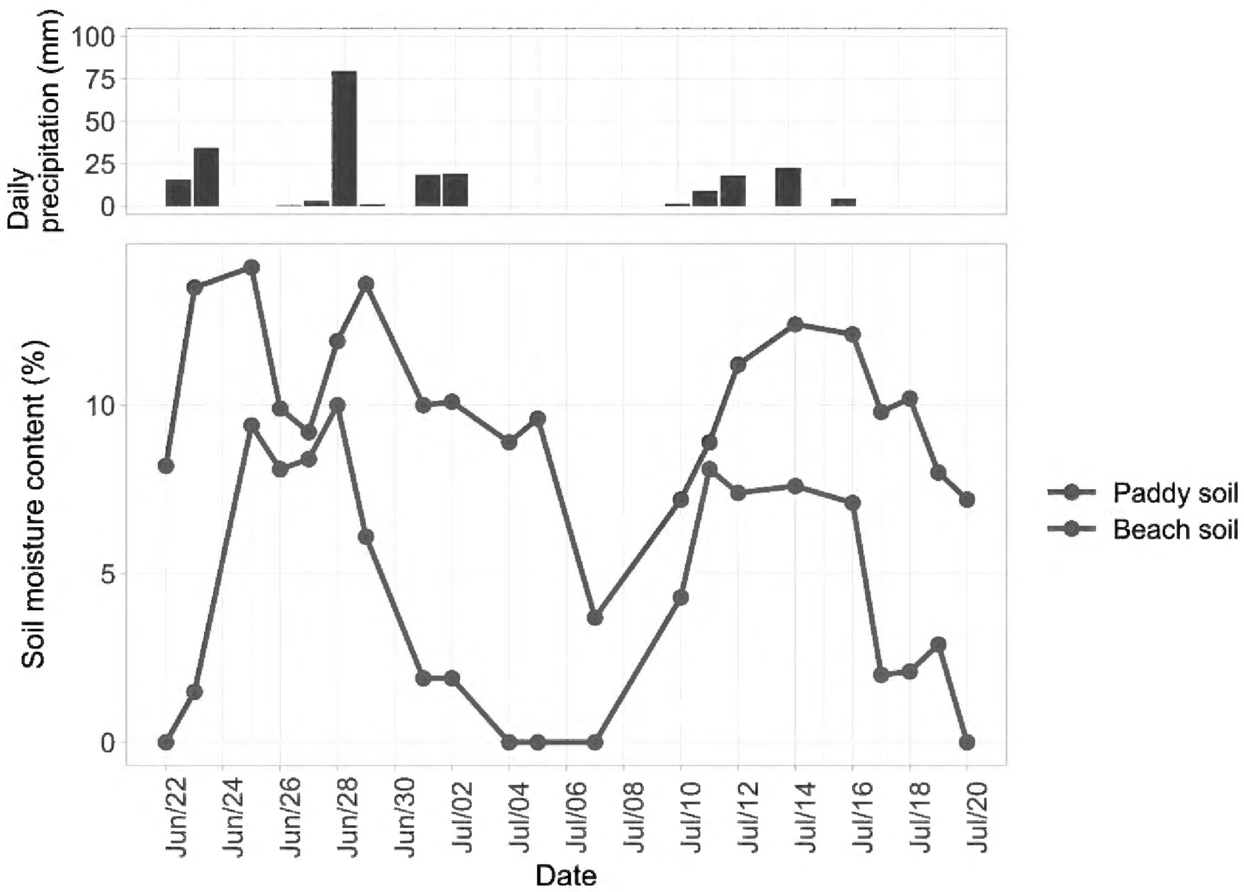

Figure 6. Daily precipitation in Kyoto City (top) and soil moisture content (bottom) from June 22th to July 20th.

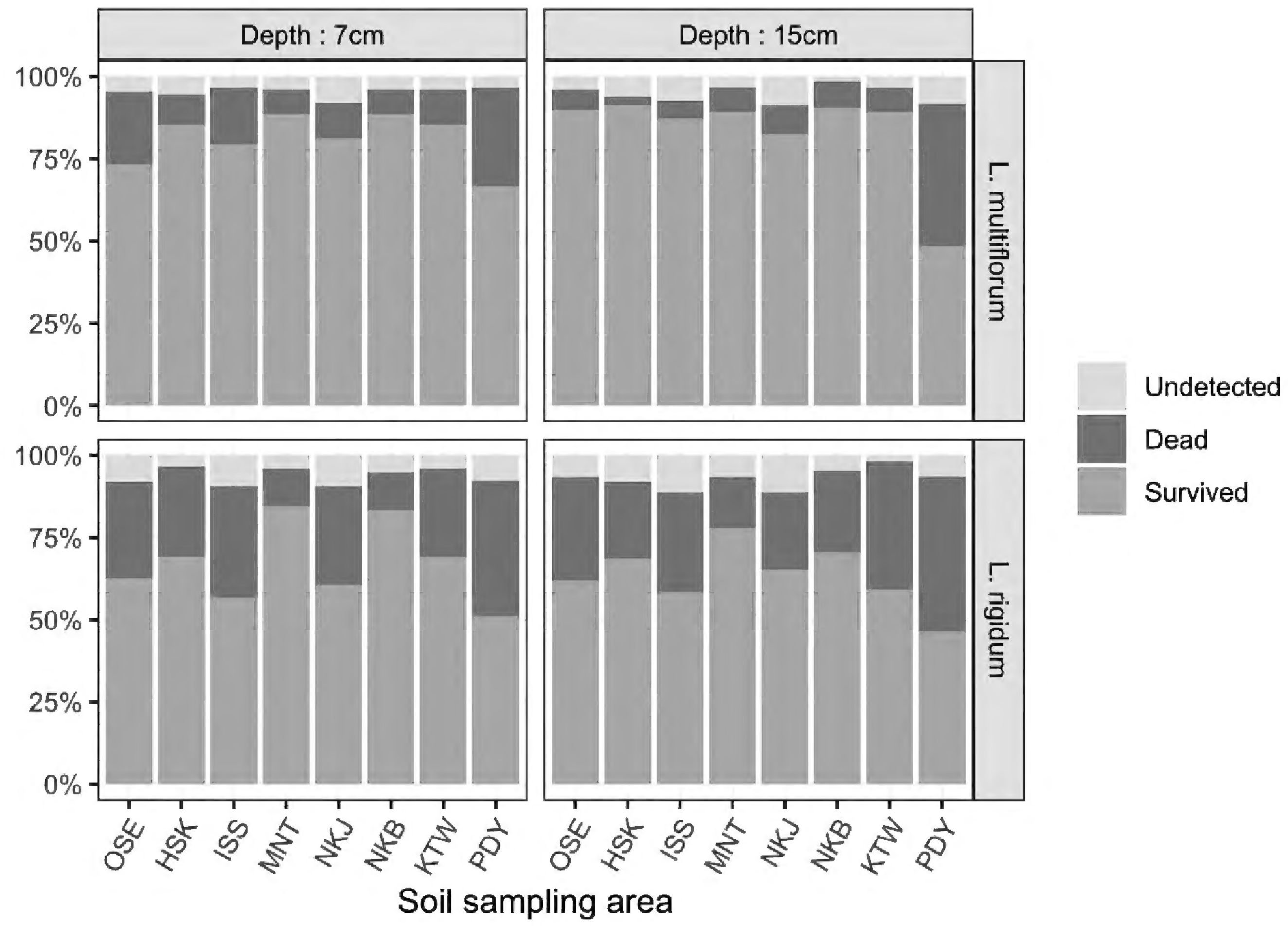

Figure 7. Breakdown of seeds retrieved from soil-filled bags. PDY represents paddy soil, whereas the remaining seven symbols indicate the collection sites of sandy beach soil samples. For further details, refer to Suppl. material 1: table S2.

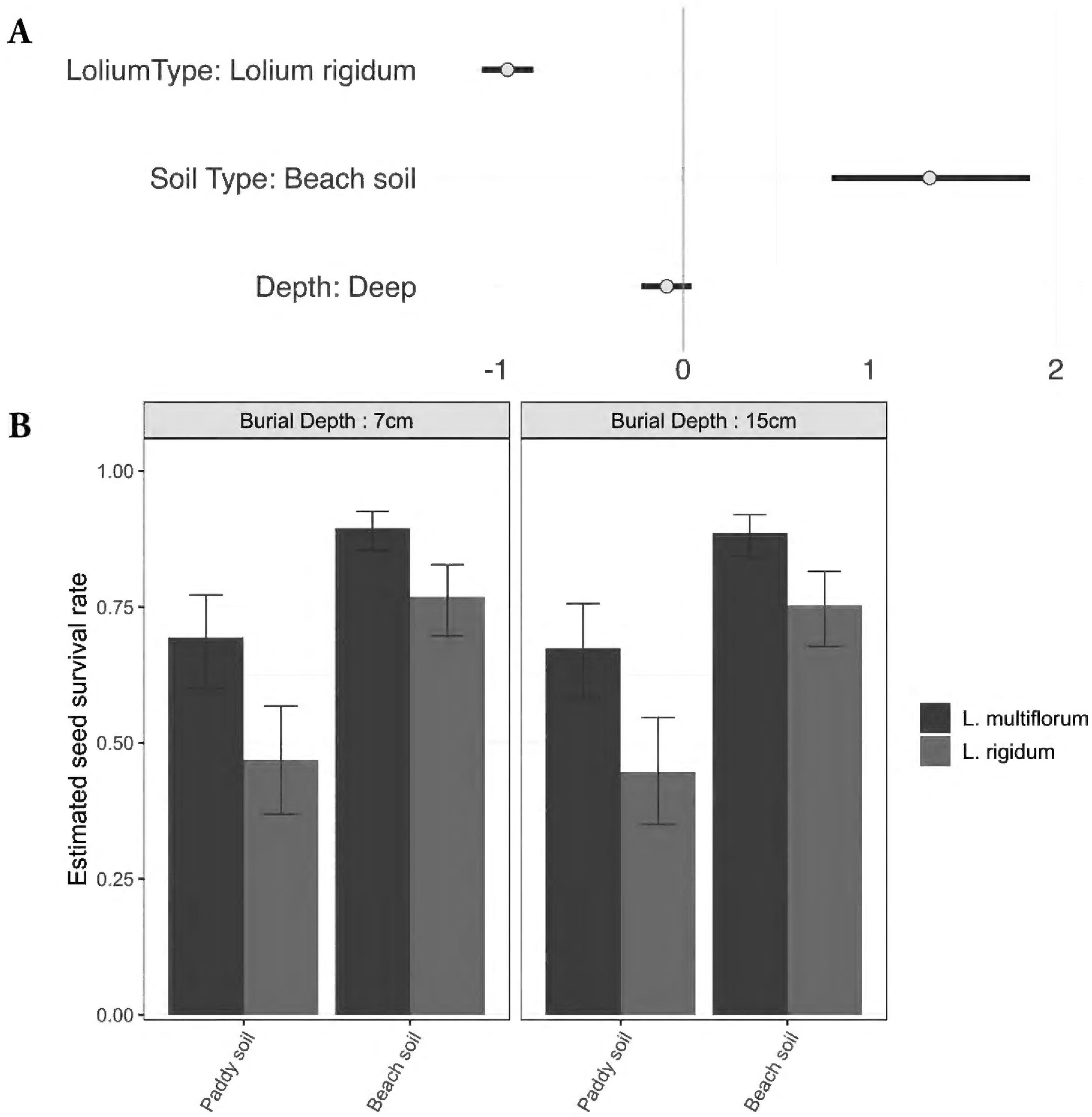

Figure 8. A estimated coefficients for survival rates (median and 95% estimate interval) of *L. rigidum* compared to *L. multiflorum* (upper), sandy beach soil compared to paddy soil (middle), and burial depth of 15 cm compared to 7 cm (lower) on a logit scale **B** estimated survival rates of *L. multiflorum* (green) and *L. rigidum* (blue) in each soil and at each depth. Error bars indicate 95% estimate intervals.

Discussion

In the present study, the MaxEnt results indicated that *L. rigidum* was less suited to the Japanese climate than *L. multiflorum*. The Japanese climatic conditions that deviated considerably from the predicted suitability range for *L. rigidum* were temperature seasonality and summer precipitation. Temperature seasonality is a determinant influencing the northern limits of plants and animals in the Northern Hemisphere (Wiens et al. 2006; Qian et al. 2022). *L. rigidum* is found in temperate zones, and as Japan is not located at the northern limit, it is currently unclear what ecological significance can be ascribed to temperature seasonality as a climatic variable that explains the distribution of *Lolium* species in Japan.

MaxEnt predicted that high summer precipitation in Japan renders the environment unsuitable for *L. rigidum*. The burial seed experiment conducted during summer revealed a higher mortality rate for *L. rigidum* seeds than for *L. multiflorum* seeds. Potential reasons for seed mortality in this experiment include seed decay or premature germination. Additionally, in real-world field conditions, various factors such as predation and fungal infections, which were not accounted for in our experiment, could further reduce seed survival rates (Ranganathan and Groot 2023). To better evaluate the fitness, the survival rate of seedlings after germination in each field should be investigated in future studies. Nevertheless, comparing our experimental findings with *L. multiflorum*, which has successfully expanded its distribution across a wide range of environments, suggests that seed decay due to heavy summer rains likely reduces the fitness of *L. rigidum* in the field.

Water availability is the primary limiting factor for terrestrial plant production (Lambers and Oliveira 2019), and soil hydrological properties at a fine scale effectively determine plant distribution (Silvertown et al. 1999). As sandy beaches are generally arid environments (Brakenhoff et al. 2019), our experimental results confirmed that under the same precipitation conditions, soil moisture content was lower in sandy soil than in paddy soil. This lower moisture content suggests that seeds of *L. rigidum* are less likely to decay in such areas, and consequently, the establishment of *L. rigidum* in Japan is possibly locally limited to sandy beaches.

L. rigidum is native to the Mediterranean region (Terrell 1968) and has emerged as a major weed problem, especially under the Mediterranean-type climate of Western Australia (Owen et al. 2014). Japan, with its monsoon climate, receives considerably higher precipitation than the aforementioned regions (annual precipitation of 1,668 mm/year in Japan versus 733 mm/year in the Perth metropolitan area, Australia) (Commonwealth of Australia 2023; The World Bank 2023). In addition, as a consequence of the widespread cultivation of rice paddies throughout the country, the soil moisture content in Japanese agricultural land is generally high. Given this context, seed decay can be considered a weed control method in Japan (Kida and Asai 2006; Aoki et al. 2012). Although the drought sensitivity and flood tolerance of seedlings have been previously assessed to understand plant distribution patterns (Engelbrecht and Kursar 2003; Jansen et al. 2005), seed moisture tolerance has mostly been neglected and underestimated.

Sandy coasts are typically arid, nutrient-poor, and highly susceptible to salt spray, sand deposition, and strong winds, all of which are limiting factors for plant establishment (Maun 1994). Dryland salinity is a major problem in agricultural areas in Australia (Briggs and Taws 2003; George et al. 2006), and *L. rigidum*, a weed that thrives in such environments, may be highly tolerant to drought and

salinity stress. Weeds that have become problematic in arid agricultural areas, not only in Australia, may have the potential to establish themselves on sandy beaches in wetter areas because of their drought and salt tolerance.

In the present study, niche modelling solely based on climate variables indicated that *L. rigidum* was not well-suited for distribution in Japan; however, it is actually expanding its distribution on sandy beaches. This suggests that climate niche modelling is insufficient for fine-scale predictions and underestimates the invasion risk of alien species in some specialised habitats. When applying SDM to finer scales, local predictors, such as soil conditions and topography, must be considered (Pearson and Dawson 2003). However, acquiring these variables over a large spatial extent is challenging (Bradley et al. 2012).

In summary, we conducted large-scale niche modelling to identify environmental factors predicted to limit the distribution of invasive species. Subsequently, we examined whether these factors actually affect the fitness of these species through manipulative experiments. Although manipulative experiments alone cannot account for all factors, focusing on environmental factors suggested by niche modelling and estimating the causality of invasion success through these experiments are highly valuable.

Conclusions

In this study, we focused on the alien *L. rigidum*, which has only expanded locally on sandy beaches in Japan, and *L. multiflorum*, which has been successfully established across various environments in Japan. We investigated the limiting factors for the distribution expansion of *L. rigidum*. Through manipulative experiments, we found that *L. rigidum* had a higher seed mortality rate, especially in paddy soil, than that of *L. multiflorum*. This result aligns with a suggestion from SDMs that the summer rainfall in Japan may be excessive for *L. rigidum.*

Predictions based solely on climate variables using SDM revealed that *L. rigidum* is not suitable for the Japanese environment. However, *L. rigidum* is actually expanding its distribution on Japanese sandy beaches. This indicates that niche modelling based on specific climate variables alone may underestimate the invasion risk of alien species. The combined use of large-scale niche modelling and manipulative experiments, as conducted in this study, demonstrates the importance of this approach for assessing the invasion risk of species in both regional and local environments.

Acknowledgements

We thank Tohru Tominaga and Shunji Kurokawa for their valuable discussions. We would like to thank Editage (www.editage.jp) for English language editing.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was partly supported by the KAKENHI Programme of the Japan Society for the Promotion of Science [grant number 20K06092].

Author contributions

Kentaro Uehira: Data curation, Formal Analysis, Investigation, Methodology, Software, Visualization, Writing - original draft. Yoshiko Shimono: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing - review and editing.

Author ORCIDs

Yoshiko Shimono https://orcid.org/0000-0002-3432-0614

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Anderson RP, Raza A (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: Preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. Journal of Biogeography 37(7): 1378–1393. https://doi.org/10.1111/j.1365-2699.2010.02290.x

Aoki M, Asai M, Sakai N (2012) Effect of summer flooding conditions on the seed viability of naturalized weeds, *Camelina microcarpa* Andrz. ex DC., *Descurainia sophia* (L.) Webb ex Prantl and *Thlaspi arvense* L. Weed Research [雑草研究] 57(3): 109–115. https://doi.org/10.3719/weed.57.109

Booth TH, Nix HA, Busby JR, Hutchinson MF (2014) BIOCLIM: The first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. Diversity & Distributions 20(1): 1–9. https://doi.org/10.1111/ddi.12144

Bradley BA, Olsson AD, Wang O, Dickson BG, Pelech L, Sesnie SE, Zachmann LJ (2012) Species detection vs. habitat suitability: Are we biasing habitat suitability models with remotely sensed data? Ecological Modelling 244(10): 57–64. https://doi.org/10.1016/j.ecolmodel.2012.06.019

Brakenhoff LB, Smit Y, Donker JJA, Ruessink G (2019) Tide-induced variability in beach surface moisture: Observations and modelling. Earth Surface Processes and Landforms 44(1): 317–330. https://doi.org/10.1002/esp.4493

Briggs SV, Taws N (2003) Impacts of salinity on biodiversity - clear understanding or muddy confusion? Australian Journal of Botany 51(6): 609–617. https://doi.org/10.1071/BT02114

Commonwealth of Australia (2023) Climate Data Online. http://www.bom.gov.au/climate/data/index.shtml [Accessed on 23.06.2023]

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, Mcclean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36(1): 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Engelbrecht BMJ, Kursar TA (2003) Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. Oecologia 136(3): 383–393. https://doi.org/10.1007/s00442-003-1290-8

Fick SE, Hijmans RJ (2017) WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37(12): 4302–4315. https://doi.org/10.1002/joc.5086

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24(1): 38–49. https://doi.org/10.1017/S0376892997000088

GBIF (2022a) GBIF Occurrence Download (*Lolium multiflorum* Lam.). https://doi.org/10.15468/dl.8y92d5 [Accessed on 29.07.2022]

GBIF (2022b) GBIF Occurrence Download (*Lolium rigidum* Gaudin.). https://doi.org/10.15468/dl.j7gcwu [Accessed on 29.07.2022]

George R, Clarke J, English P (2006) Modern and palaeogeographic trends in the salinisation of the Western Australian Wheatbelt. ASEG Extended Abstracts 2006(1): 1–22. https://doi.org/10.1071/ASEG2006ab049

Green RH (1979) Sampling Design and Statistical Methods for Environmental Biologists. John Wiley, New York.

Hayes KR, Barry SC (2008) Are there any consistent predictors of invasion success? Biological Invasions 10(4): 483–506. https://doi.org/10.1007/s10530-007-9146-5

Heap I (2023) The International Herbicide-Resistant Weed Database. http://www.weedscience.org/ [Accessed on 08.05.2023]

Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30(6): 751–777. https://doi.org/10.1177/0309133306071957

Higuchi Y, Shimono Y, Tominaga T (2017) The expansion route of ryegrasses (*Lolium* spp.) into sandy coasts in Japan. Invasive Plant Science and Management 10(1): 61–71. https://doi.org/10.1017/inp.2017.1

Hirata M, Higuchi Y, Matsuo A, Sato MP, Suyama Y, Kiyoshi T, Konuma A, Tominaga T, Shimono Y (2023) Introduction pathways and evolutionary mechanisms of alien species of Lolium spreading across sandy coasts in Japan. Journal of Ecology 111(12): 2583–2596. https://doi.org/10.1111/1365-2745.14206

Hui C, Richardson DM, Landi P, Minoarivelo HO, Garnas J, Roy HE (2016) Defining invasiveness and invasibility in ecological networks. Biological Invasions 18(4): 971–983. https://doi.org/10.1007/s10530-016-1076-7

Humphreys M, Feuerstein U, Vandewalle M, Baert J (2010) Ryegrasses. In: Boller B, Posselt U, Veronesi F (Eds) Fodder Crops and Amenity Grasses. Handbook of Plant Breeding, Vol. 5. Springer, New York, 211–260. https://doi.org/10.1007/978-1-4419-0760-8_10

Jansen C, Van De Steeg HM, De Kroon H (2005) Investigating a trade-off in root morphological responses to a heterogeneous nutrient supply and to flooding. Functional Ecology 19(6): 952–960. https://doi.org/10.1111/j.1365-2435.2005.01049.x

Japan Meteorological Agency (2024) Japan Meteorological Agency. https://www.jma.go.jp/jma/indexe.html [Accessed on 12.07.2024]

Kida Y, Asai M (2006) Effect of summer flooding on wild oat and Italian ryegrass seed viability. Weed Research [雑草研究] 51(2): 87–90. https://doi.org/10.3719/weed.51.87

Lambers H, Oliveira RS (2019) Plant Water Relations. In: Plant Physiological Ecology. Springer International Publishing, Cham, 187–263. https://doi.org/10.1007/978-3-030-29639-1_5

Liebl R, Worsham AD (1987) Interference of Italian Ryegrass (*Lolium multiflorum*) in Wheat (*Triticum aestivum*). Weed science society of America 35(6): 819–823. https://doi.org/10.1017/S0043174500079406

Liu C, Wolter C, Xian W, Jeschke JM (2020) Most invasive species largely conserve their climatic niche. Proceedings of the National Academy of Sciences of the United States of America 117(38): 23643–23651. https://doi.org/10.1073/pnas.2004289117

Maun MA (1994) Adaptations enhancing survival and establishment of seedlings on coastal dune systems. Vegetatio 111(1): 59–70. https://doi.org/10.1007/BF00045577

Merow C, Smith MJ, Silander Jr JA (2013) A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. Ecography 36(10): 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Owen MJ, Martinez NJ, Powles SB (2014) Multiple herbicide-resistant *Lolium rigidum* (annual ryegrass) now dominates across the Western Australian grain belt. Weed Research 54(3): 314–324. https://doi.org/10.1111/wre.12068

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography 12(5): 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Phillips SJ (2008) Transferability, sample selection bias and background data in presence-only modelling: A response to Peterson et al. (2007). Ecography 31(2): 272–278. https://doi.org/10.1111/j.0906-7590.2008.5378.x

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. Ecography 31(2): 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Phillips SJ, Dudík M, Schapire RE (2004) A maximum entropy approach to species distribution modeling. Proceedings, Twenty-First International Conference on Machine Learning - ICML, Banff, Canada. https://doi.org/10.1145/1015330.1015412

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190(3–4): 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. Annual Review of Environment and Resources 35(1): 25–55. https://doi.org/10.1146/annurev-environ-033009-095548

Qian H, Zhang Y, Ricklefs RE, Wang X (2022) Relationship of minimum winter temperature and temperature seasonality to the northern range limit and species richness of trees in North America. Journal of Geographical Sciences 32(2): 280–290. https://doi.org/10.1007/s11442-022-1947-z

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.r-project.org/

Ranganathan U, Groot SPC (2023) Seed Longevity and Deterioration. In: Dadlani M, Yadava DK (Eds) Seed Science and Technology. Springer, Singapore, 91–108. https://doi.org/10.1007/978-981-19-5888-5_5

Richardson DM, Pyšek P (2006) Plant invasions: Merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30(3): 409–431. https://doi.org/10.1191/0309133306pp490pr

Rodriguez AM, Jacobo EJ, Deregibus VA (1998) Germination behaviour of Italian ryegrass in flooding pampa rangelands. Seed Science Research 8(4): 521–528. https://doi.org/10.1017/S0960258500004499

Shimono Y, Shimono A, Oguma H, Konuma A, Tominaga T (2015) Establishment of *Lolium* species resistant to acetolactate synthase-inhibiting herbicide in and around grain-importation ports in Japan. Weed Research 55(1): 101–111. https://doi.org/10.1111/wre.12120

Silvertown J, Dodd ME, Gowing DJG, Mountford JO (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400(6739): 61–63. https://doi.org/10.1038/21877

Sønderskov M, Somerville GJ, Lacoste M, Jensen JE, Holst N (2020) DK-RIM: Assisting Integrated Management of *Lolium multiflorum*, Italian Ryegrass. Agronomy 10(6): 1–15. https://doi.org/10.3390/agronomy10060856

Stan Development Team (2024) RStan: the R interface to Stan. R package version 2.32.5. https://mc-stan.org/

Terrell EE (1968) A Taxonomic Revision of the Genus *Lolium*. Agricultural Research Service, U.S. Dept. of Agriculture, Washington, D.C. 1392: 1–65.

The World Bank (2023) Average precipitation in depth (mm per year). https://data.worldbank.org/indicator/AG.LND.PRCP.MM [Accessed on 27.06.2023]

Vanagas G (2004) Receiver operating characteristic curves and comparison of cardiac surgery risk stratification systems. Interactive Cardiovascular and Thoracic Surgery 3(2): 319–322. https://doi.org/10.1016/j.icvts.2004.01.008

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, Andriopoulos P, Arianoutsou M, Bazos I, Kokkoris I, Yannitsaros A, Zikos A, Augustin S, Cochard PO, Lopez-Vaamonde C, Sauvard D, Yart A, Bacher S, Bretagnolle F, Gasquez J, Chiron F, Kark S, Shirley S, Clergeau P, Cocquempot C, Coeur d'Acier A, Dorkeld F, Migeon A, Navajas M, David M, Delipetrou P, Georghiou K, Desprez-Loustau ML, Didziulis V, Essl F, Galil BS, Hejda M, Jarosik V, Pergl J, Perglová I, Kühn I, Winter M, Kühn PW, Marcer A, Pino J, McLoughlin M, Minchin D, Panov VE, Pascal M, Poboljsaj K, Scalera R, Sedlácek O, Zagatti P (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment 8(3): 135–144. https://doi.org/10.1890/080083

Vitousek PM (1990) Biological Invasions and Ecosystem Processes: Towards an Integration of Population Biology and Ecosystem Studies. Oikos 57(1): 7–13. https://doi.org/10.2307/3565731

Wiens JJ, Graham CH, Moen DS, Smith SA, Reeder TW (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: Treefrog trees unearth the roots of high tropical diversity. American Naturalist 168(5): 579–596. https://doi.org/10.1086/507882

Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: Assessing the assumptions and uncertainties. Proceedings of the National Academy of Sciences of the United States of America 106(supplement_2): 19729–19736. https://doi.org/10.1073/pnas.0901639106

Williamson M, Fitter A (1996) The Varying Success of Invaders. Ecology 77(6): 1661–1666. https://doi.org/10.2307/2265769

Yoshioka A, Takada M, Washitani I (2011) Facilitation of a native pest of rice, *Stenotus rubrovittatus* (Hemiptera: Miridae), by the non-native *Lolium multiflorum* (Cyperales: Poaceae) in an agricultural landscape. Environmental Entomology 40(5): 1027–1035. https://doi.org/10.1603/EN11032

Supplementary material 1

Supplementary information

Author: Kentaro Uehira

Data type: docx

Link: https://doi.org/10.3897/neobiota.96.122752.suppl1